Inferences of breeding patterns from moult data of lovebirds *Agapornis* spp. at Lake Naivasha, Kenya

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Since the introduction of hybrid lovebirds to Lake Naivasha in the 1960s, these birds have spread to encircle the lake, their numbers increasing to more than 6000 by 1986 (Thompson 1989). During mark-recapture studies, the opportunity was taken to study their moult patterns over 12 months of fieldwork. At Naivasha, lovebird nests are usually placed high up in *Acacia xanthophloea* trees and constructed with long entrance tunnels making nest inspection difficult. Instead, moult data were used to examine breeding seasons indirectly since feather renewal is closely linked with breeding in parrots (Forshaw 1981).

Methods

Study Area

Lake Naivasha lies in the Kenyan Rift Valley between latitudes 0°50S and 0°40S and longitudes 36°15E and 36°25E. The lake has a circumference of approximately 75 km with a warm and semi-arid climate and an average annual rainfall of 627 mm. Although rainfall is unpredictable, the general pattern is of relatively heavy rains in April–May with lighter falls in other months. Surrounding the lake is a belt of forest composed almost entirely of acacia trees *Acacia xanthophloea* combined or interspersed with areas of irrigated cultivation or grassland for intensive livestock management.

Moult Scoring

The moult status of each wing was scored separately by assigning a numerical value to each primary feather according to the internationally accepted 0–5 scale (Ginn & Melville 1983). A zero was assigned to an old feather, "1" a missing feather or emergent pin, "2" a feather one-third grown, "3" two-thirds grown, "4" three-quarters grown and "5" a nearly complete or completely grown feather. In cases where the moult score differed between wings, the average of the two scores was used for moult rate calculations. By using the calculated average moult rate, the date of moult initiation in moulting birds was determined and therefore the theoretical date of breeding cessation.

Primary moult was considered as interrupted if all feathers were fully grown and no basal sheath was present on newly grown feathers. While moult interruption appears to occur for a variety of reasons in different species, it is usually associated either with breeding or migration (Harper 1984). This is generally thought to be due to the metabolic incompatibility of these processes so that they are programmed to occur at different times (Foster 1975, Payne 1969, Jones 1978, Miller 1961). Since lovebirds are not migratory, interruption of their moult is interpreted here as an indication of breeding activity.

Results

Moult pattern

Lovebirds, like all parrots, renew their primaries from the centre outwards, usually beginning at the sixth primary. Taking the moult of both wings separately, out of 102 cases where initiation of primary moult could be observed, 0.9 per cent, 15.6 per cent, 82.3 per cent and 0.9 per cent of the birds began their moult at the fourth, fifth, sixth and seventh primaries, respectively. The usual pattern was then to drop feathers progressively on either side of the moult focus (Payne 1972) finishing by regrowing the inner- or outermost primary last.

Moult rate

Five lovebirds were recaptured 4, 10, 16, 17 and 192 days after being ringed and their moult scores had progressed by 1.5, 1, 4, 4 and 24 points respectively. This gives an average moult point with a standard deviation of 3.1 days per point. It is assumed that the relationship between the increase in moult score with time is linear so that on average the primary moult takes 290 days (5.8 x 50) for completion. The 95 per cent confidence limits for moult rate (using the appropriate statistics, d.f. = 4) is given by 5.8 + 3.9 days per point or between 95 and 485 days for a complete moult cycle.

Breeding

Over the study period, a total of 164 moulting lovebirds were captured. Numbers caught and percentages of moulting birds in total monthly samples are presented in Table 1. Using the calculated average moult rate, the numbers of birds initiating their moult (and hence ceasing breeding) in each month are presented in Fig. 1a. An adjustment to this histogram is necessary, however, because birds initiating their moult in some months had a longer period of time over which they might have been caught than others. For example, birds initiating their moult in June 1986 had available only one month over which they could have been caught, whereas those initiating in May 1986 had two months. Since the average time to complete a moult cycle is 290 days (roughly ten months) the longest period of time available to capture while moulting is ten months. This would have corresponded to birds initiating their moult in August and September 1985 except that no collections were made in January 1986. Therefore, these August and September birds only had nine months available for capture instead of ten. The correction factor was derived from the number of months available for capture and the lower histogram generated by

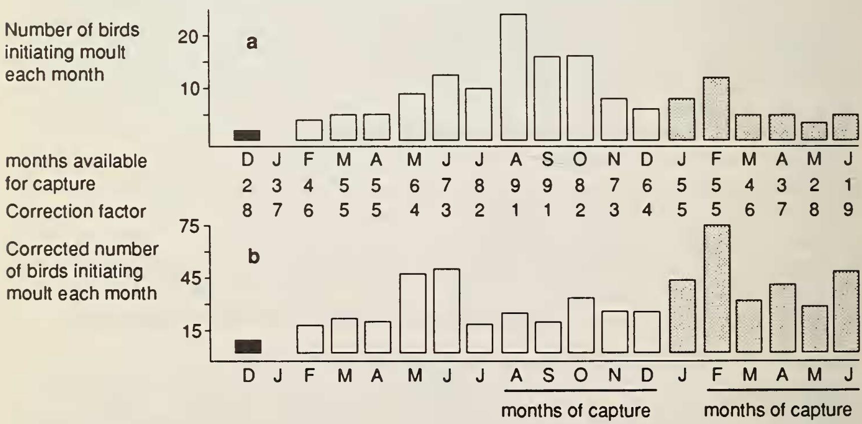

Fig. 1. *The use of primary moult to detect any breeding seasonality. The lower histogram (b) gives the derived number of sampled birds in each month initiating their moult and hence their cessation of breeding. Black is 1984, white 1985, grey 1986.*

the multiplication of each month in Fig. 1a by its correction factor. For example, the number of birds initiating their moult in August and September 1985 was multiplied by a factor of one, those in July and October by two, and so on. The resulting histogram (Fig. 1b) gives an unbiased estimate of the proportion of lovebirds ceasing to breed in each month, as derived from moult data.

A runs test showed that the initiation of moult in captured lovebirds was not randomly distributed ($P < 0.05$ one-tailed test) with time, but was concentrated towards the latter half of the study period. The percentages of captured lovebirds with interrupted moult in each month are presented in Table 1. A runs test showed that the percentage of lovebirds with interrupted moult did vary randomly throughout the study period.

Table 1. *Monthly moult data for lovebirds caught over the study period*

Month	Number caught	Percentage moulting	Percentage with interrupted moult
August	58	16	1.7
September	94	14	1.0
October	109	28	2.8
November	120	37	3.3
December	31	13	0
January*	–	–	–
February	64	41	6.3
March	57	40	1.8
April	46	39	3.1
May	19	26	5.3
June	42	62	21.4

*No lovebirds caught in January

A correlation analysis was performed on monthly breeding and rainfall data. For this, breeding data from Fig. 1b were shifted to the left by one month since these data represent the frequencies of birds ceasing to breed in each month rather than the frequency actually breeding. Monthly rainfall was then compared with the following month's level of breeding cessation. The correlation ($r = -0.185$) was not significant at the 0.05 level of probability.

Discussion

It is a pity that so few lovebirds were recaptured at different stages of their moult since the following arguments concerning breeding seasons are based on assumptions made about moult rate of the five individuals actually recaptured. Moult rate in lovebirds (and parrots in general) may be particularly variable due to its relatively slow progress. Nevertheless, while the details of Fig. 1b may be subject to error due to the small sample size in moult rate calculations, there is little doubt that lovebirds are capable of breeding at Naivasha in any month of the year.

The cause of the significant increase in breeding activity towards the end of the study period is unknown. A longer period of study is necessary to ascertain the cause of breeding peaks since, as Fig. 1b suggests, such patterns may be dependant on factors other than regular annual events, but rather on events which may occur over a longer period of time, such as unusually high rainfall affecting food availability. The independence of breeding from regular seasonal events is further suggested by interrupted moult data since over the study period, the frequency of interrupted moult varied randomly. The lack of annual breeding peaks may be due to the agricultural nature of Naivasha's habitat since irrigation has probably caused food availability to be somewhat independent of rainfall—the most noticeable climate effect in tropical regions (Brown & Britton 1980) likely to affect breeding.

It is likely that some variation in intensity of breeding occurs around the lake according to local conditions. Rainfall at the lake tends to be extremely patchy, especially in drier years, so that marked differences in food availability within short distances are possible. Patchy irrigation also enhances locally uneven food supplies. Since lovebirds at Lake Naivasha were found to have an average home range of only 2.6 km (Thompson 1987), their breeding behaviour may be dependent on their ability to forage outside these locally abundant food patches. For example, in Panama, Kalma (1970) found quite different breeding patterns of the Rufous-collared Sparrow *Zonotrichia capensis* within a distance of only three kilometres depending on the condition and dryness of local grasslands. Since lovebirds were captured all around the lake, local variations in breeding seasonality caused by a temporally and spatially patchy food supply could explain their apparent ability to breed at any time of the year.

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